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CLOACAL RESORPTION OF SALT AND WATER IN THE GALAH (*CACATUA ROSEICAPILLA*)

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SUMMARY

1. The transmural net flow of salt and water in the coprodeum and large intestine of the Galah (*Cacatua roseicapilla*), an Australian xerophilic parrot, was measured by an *in vivo* perfusion technique. The main goal of the study was to understand what happens when the hyperosmotic ureteral urine formed in the dehydrated state is regurgitated into the cloaca. Buffered perfusion fluids, hyper- and isosmotic to plasma, with varying NaCl and KCl concentrations, were used. [^{14}C]polyethylene glycol served as an unabsorbable water marker.

2. The cloacal Na^+ and Cl^- absorption rates were nearly parallel and at low luminal concentrations roughly proportional to the intraluminal concentrations. At higher concentrations the Na^+ absorption rate showed saturation. The maximal Na^+ flow was 217 μequiv/kg.hr, the concentration at half maximal flow 181 m-equiv/l. The Na^+ absorption rate was not impaired by a high K^+ concentration. K^+ was secreted into the intestine, except at high intraluminal K^+ concentrations where resorption was observed.

4. The apparent osmotic permeability coefficient was 0·85 μl./kg.hr.m-osmole at an average osmotic difference of 446 m-osmole between lumen and plasma; it was higher at lower differences. In the (near) absence of an osmotic difference across the cloacal epithelium the solute-linked water flow was 5·0 μl. H_2O/μequiv Na^+.

5. It is concluded that the hyperosmotic ureteral urine formed in the dehydrated state can pass into the cloaca without a water loss. A Na^+ absorption of around 70% of the ureteral output is likely.

INTRODUCTION

In birds the ureteral urine runs into the coprodeum and large intestine (Skadhauge, 1968, 1972). Previous investigations (Skadhauge, 1967; Bindslev & Skadhauge, 1971*a*, *b*) have shown that the hyperosmotic ureteral urine formed in the dehydrated fowl (*Gallus domesticus*) can move into the coprodeum and large intestine without a further water loss. This is due to a solute-linked water flow caused by NaCl absorption. Computer calculations (Skadhauge & Kristensen, 1972; Skadhauge, 1973) predicted that birds with a higher renal concentrating ability such as the Budgerygah (*Melopsittacus undulatus*) (Krag & Skadhauge, 1972) could not survive if fed dry seeds alone since the calculated water loss was too large. The Budgerygah could, however, survive without water for months (Cade & Dybas, 1962; Greenwald, Stone & Cade, 1967; Krag & Skadhauge, 1972). The computer calculation was based on the cloacal transport parameters of the domestic fowl on a weight basis. Due to its small size cloacal perfusion studies were difficult in the Budgerygah.

The aim of the present study was to measure the cloacal salt and water transport in a large xerophilic seed eating bird which had a good concentrating ability and no salt gland. *A priori* parrots from Australian arid zones would be considered suitable. The Galah (*Cacatua roseicapilla*) was chosen since the urine to plasma osmotic ratio was found to 2·6 in the dehydrated state (Skadhauge, 1974*a*). It is of convenient size, around 300 g, and its drinking pattern (Fisher, Lindgren & Dawson, 1972) and food consumption (Serventy & Whittell, 1967) have already been studied. Furthermore, its temperature relations and evaporation and ability to drink saline is under study (W. R. Dawson, personal communication).

METHODS

Animals. The experiments were carried out in January–March 1973 in Perth, W. Australia on birds purchased from local dealers. Nine birds were kept in a large aviary until the experiments. They were fed dry seeds supplemented with lettuce. Tap water and cuttle bones were available. Three birds were dehydrated for 48 hr with an average weight loss of 12 %. They had free access to dry seeds. These contained 13·8 % water.

Operation. The Galahs were weighed, and 200 mg phenobarbitone/kg body wt. was injected I.M. When good anaesthesia was obtained the birds were placed on their back, the abdomen opened and a thin catheter inserted into the large intestine at an average distance along the gut of 27 ± 1 mm from the urodeum. The abdomen was closed. The anus was opened and a catheter (the top of a Beckman microtube) inserted into the coprodeum and a purse string suture placed in the submucosa at the junction of urodeum and coprodeum. This permitted perfusion of the coprodeum and large intestine from the oral end. The intestine was thoroughly rinsed with body warm isosmotic saline, and a perfusion with an experimental solution started

at a rate of 0·5–0·9 ml./hr delivered by a precision perfusion pump (Braun Unita II) after initial rinsing with the perfusate. After 1½ hr equilibrium was established (Fig. 1) and the outflow concentrations were measured on two to three consecutive samples taken with approximately 25 min interval. In similar perfusion experiments on *Gallus domesticus* equilibrium was also reached after 1½ hr (Bindslev & Skadhauge, 1971*a*). Two to four perfusions were carried out on each bird. A total of thirty-four experiments were performed. A blood sample was drawn into heparinized syringes before and after the experiments. During some of the experiments ureteral urine was collected immediately after appearance by suction into a capillary. At the end the bird was decapitated and the intestine removed for planimetric determination of the area of the perfused segment.

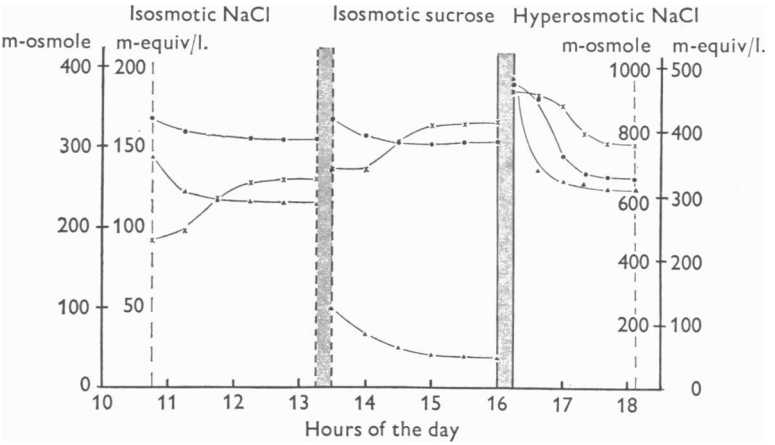

Fig. 1. Effluent concentrations of the cloacal perfusate as functions of time. Expt. no. 5, 14 February 1973. Experiments with isosmotic NaCl, isosmotic sucrose, and hyperosmotic NaCl are presented. Equilibrium is reached after approximately 1½ hr. ●, Osmolality; ×, PEG; ▲, Na.

Perfusion fluids. Five different perfusion fluids were used. All contained approximately 1 μc [^{14}C]polyethylene glycol (PEG) mol. wt. 4000, New England Nuclear Corp. Lot no. 318–234, and KCl, 9; $MgSO_4$, 2; $CaCl_2$, 1; $KHCO_3$, 25; and KH_2PO_4, 6 m-equiv/l., and NaCl (and sucrose) to final concentrations as reported in Table 1. The pH was found to 7·1–7·3.

Analyses. Osmolality was measured on the Knauer freezing point osmometer with NaCl solutions as standards; Na^+ and K^+ were measured on the Eppendorf flame photometer, Cl^- on the Buchler–Cotlove chloridometer. ^{14}C was analysed on the Packard Tri Carb spectrometer. As scintillation fluid, was used the Hall & Cocking (1965) solution. Most analyses were carried out in duplicate.

Calculations. The transmural flows in the perfused segment of water, Na^+, K^+, and Cl^- have been calculated from the incoming and the equilibrium concentrations of ions and PEG and the inflow rate (Bindslev & Skadhauge, 1971*a*). The transport rates have been calculated per kg body wt. (before dehydration) and hour. Mean values ± S.E. are reported throughout.

TABLE 1. Composition of perfusion fluids

	Osmolality (m-osmole)	Na (m-equiv/l.)	K (m-equiv/l.)	Cl (m-equiv/l.)
NaCl, isosmotic	335	143	40	154
NaCl, hyperosmotic I	950	485	40	496
NaCl, hyperosmotic II	770	385	40	396
Sucrose, isosmotic	335	50	40	61
KCl, isosmotic	335	50	135	156

(Concentrations of other ions are given in Methods)

TABLE 2. Osmotic and ionic concentrations of plasma and urine (mean ± S.E.)

		Osmolality (m-osmole)	Na (m-equiv/l.)	Cl (m-equiv/l.)	K (m-equiv/l.)	No. of expt.
Plasma	Normal	334 ± 4	143 ± 1·7	120 ± 1·3	4·8 ± 0·2	9
	Dehydrated	388 ± 10	157 ± 3·1	134 ± 0·3	4·5 ± 0·5	3
Urine	Normal	701 ± 79	205 ± 38	162 ± 21	98 ± 25	5
	Dehydrated	973 —	134 —	49 —	369 —	2

Control experiments

Area of perfused segment in relation to body weight. The average body weight before dehydration was 291 ± 10 g, and the average perfused area 2·84 ± 0·23 cm^2. The perfused segment is identical to that with which the ureteral urine normally comes into contact. A clear boundary between the oral end of the large intestine and the lower end of the small intestine is, however, not macroscopically visible due to the absence of caeca. The simple resorptive area is approximately 1 cm^2/100 g.

Plasma and urine osmolality and electrolyte concentrations. These values are reported in Table 2. Dehydration resulted approximately in a 10 % increase in plasma osmolality and NaCl concentrations; the urine osmolality was equal to that of the lower end of the droppings collected in the dehydrated state (Skadhauge, 1974*a*).

Loss of water marker. In none of the twelve birds could a ^{14}C concentration above 0·1 % of the perfusion fluid concentration be detected in plasma after the termination of the experiments. In seven of the experiments the urine was collected and a measurable concentration of ^{14}C found to 0·8 ± 0·2 % of the equilibrium perfusion concentration. The urine was collected during the last perfusion period. Its average osmolality was 785 ± 74 m-osmole. If the urine flow at this osmolality was 200 µl./hr and the perfusion rate 0·5 µl./hr the ^{14}C lost in the urine would be 0·3 % of the infused amount.

Measurement of equilibrium concentrations. In order to assess the degree of equilibrium attained, the osmotic, ionic (Na^+, K^+, Cl^-) and PEG concentrations of the last sample in each of the thirty-four experiments was calculated as fractions of the concentrations of the previous sample. The five fractional values were then averaged. The mean of these average values was 1·001 ± 0·003. The mean of the twelve experiments with perfusion of isosmotic NaCl was 1·007 ± 0·004. The mean of the twelve hyperosmotic NaCl perfusion experiments was 1·008 ± 0·003. Thus, no systematic difference is seen from experiments in which the incoming fluid is always concentrated to experiments in which it is diluted.

The equilibrium was, however, only just reached. In the sixteen experiments with

isosmotic NaCl and sucrose where the PEG concentration always rose and the Na^+ and Cl^- concentrations always fell the average PEG ratio was $1{\cdot}025 \pm 0{\cdot}009$, the average NaCl ratio was $0{\cdot}967 \pm 0{\cdot}011$.

RESULTS

The osmotic and ionic concentrations at equilibrium are reported in Table 3. For the same perfusion solutions some difference is seen in the equilibrium concentrations between normally hydrated and dehydrated birds due to different plasma osmolalities (Table 2). Since the electrolyte transport rates were not significantly different for the different perfusion fluids due to the state of hydration both the transport rates and the equilibrium concentrations were averaged. The electrolyte and the water transport observations are reported in detail below.

Electrolyte transport

The electrolyte transport rates in the individual isosmotic NaCl perfusion experiments are reported in Table 4, the average transport rates for the different perfusion fluids in Table 5.

The dependence of the Na^+, K^+, and Cl^- transport upon the arithmetic mean of the incoming and the average equilibrium concentrations is illustrated in Fig. 2.

Na transport

From Fig. 2 it will appear that the Na^+ transport shows saturation with increased intraluminal sodium concentration. The Lineweaver–Burke plots of the data showed an almost linear relationship ($r = 0{\cdot}99$). The maximal Na transport rate ($J_{Na_{max}}$) was calculated to 217 μequiv/kg.hr, the intraluminal concentration at half maximal flow ($C_{Na_{\frac{1}{2}}}$) to 181 m-equiv/l. The $J_{Na_{max}}$ is fairly close to the value found in the domestic fowl, the $C_{Na_{\frac{1}{2}}}$ larger (Bindslev & Skadhauge, 1971*b*). From Table 4 it will appear that in the three experiments in this study performed on dehydrated birds perfused with isosmotic NaCl solutions the Na^+ absorption rate was not larger than in the normally hydrated birds. In the few experiments performed it was lower.

The chloride absorption rate was, in the range of intraluminal chloride concentrations tested, fairly proportional to the intraluminal concentration; the linear regression line had a coefficient of correlation of 0·99 (Fig. 2). In the perfusion experiments with a high intraluminal KCl concentration the chloride absorption seemed to be inhibited (Table 5). Thus under most experimental conditions the Na^+ and Cl^- absorption rates were parallel, except when a K^+ absorption occurred due to a high intraluminal K^+ concentration.

Potassium was secreted into the intestinal lumen in all experiments with incoming K^+ concentrations of 40 m-equiv/l. Only in the high K^+ concentration experiments was a K^+ absorption taking place (Table 5).

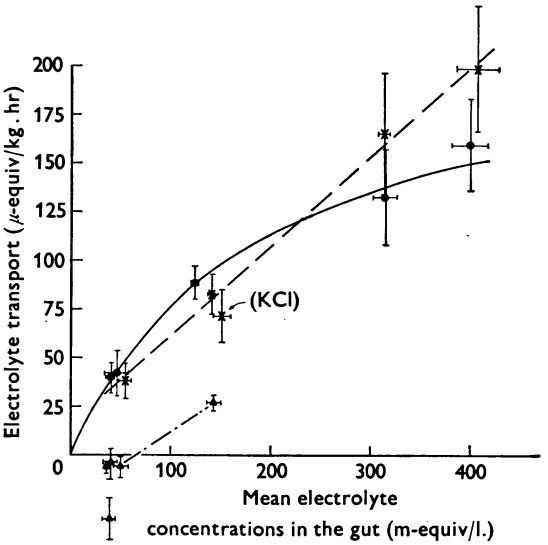

Fig. 2. Electrolyte transport rates as functions of the average electrolyte concentrations in the gut. The Na absorption rate shows saturation kinetics. The continuous line is made from the Lineweaver–Burke plot of the data. The chloride absorption rate (interrupted lines) appears linearly related to the concentration, but the scatter is large at high concentrations. A high K concentration '(KCl)' impairs the chloride absorption. K is secreted except when the luminal concentration is high. ●, Na^+; —, $y = (217x)/(181+x)$, $r = 0{\cdot}999$. ×, Cl^-; — —, $y = 0{\cdot}46x + 16$; $r = 0{\cdot}998$. ▲, K^+, —·—.

TABLE 3. Equilibrium osmolality and ionic concentrations (mean ± S.E.)

Perfusion fluid	Adaptation	Osmolality (m-osmole)	Na (m-equiv/l.)	Cl (m-equiv/l.)	K (m-equiv/l.)	No. of expt.
NaCl, isosmotic	Normal hydration	323 ± 5	98·7 ± 9·2	120 ± 6·5	59·4 ± 6·8	9
NaCl, isosmotic	Dehydrated	367 ± 4	120 ± 7·5	150 ± 8·6	62·1 ± 8·2	3
KCl, isosmotic	Normal hydration	331 ± 9	22·4 ± 3·7	131 ± 11·5	150 ± 3·0	3
KCl, isosmotic	Dehydrated	361 ± 4	37·8 ± 3·0	158 ± 7·2	149 ± 6·9	3
Hyperosmotic I	Normal hydration	603 ± 52	295 ± 34	296 ± 38	31·2 ± 1·8	5
Hyperosmotic I	Dehydrated	711 ± 43	344 ± 22	353 ± 34	34·0 ± 2·6	3
Hyperosmotic II	Normal hydration	522 ± 25	244 ± 12	238 ± 18	40·4 ± 2·5	4
Sucrose, isosmotic	Normal hydration	330 ± 11	38·8 ± 12·2	46·6 ± 5·9	38·8 ± 3·5	4

TABLE 4. Water and electrolyte transport rates in the isosmotic NaCl perfusion experiments

Expt. no.	H_2O (μl./kg.hr)	Na (μequiv/kg.hr)	K (μequiv/kg.hr)	Cl (μequiv/kg.hr)
2	313	65·7	21·6	95·9
3	420	74·0	16·0	76·6
4	450	78·5	−2·9	82·5
5	558	102·0	11·7	94·9
6	568	93·0	5·9	105·3
9	443	111·4	−19·1	84·3
10	154	80·3	−36·6	69·7
11	521	100·6	−9·7	119·2
14	484	154·0	−57·1	149·6
8	215	34·9	−10·3	44·1
12	549	94·7	−6·2	81·9
13	354	58·5	−15·1	40·3

Expts. 8, 12 and 13 are performed on dehydrated birds, the other on normally hydrated birds. A − sign denotes secretion into the intestine.

TABLE 5. Electrolyte transport rates for the different perfusion solutions (mean ± S.E.)

	Na (μequiv/kg.hr)	Cl (μequiv/kg.hr)	K (μequiv/kg.hr)	No. of expt.
NaCl, isosmotic	87·9 ± 8·6	82·1 ± 10·8	−6·0 ± 5·9	12
KCl, isosmotic	40·1 ± 8·2	72·4 ± 15·2	26·5 ± 4·0	6
NaCl hyperosmotic I	158·9 ± 24·4	197·9 ± 34·3	−5·6 ± 3·2	8
NaCl hyperosmotic II	131·5 ± 25·2	165·0 ± 34·5	−32·4 ± 11·9	4
Sucrose, isosmotic	42·1 ± 12·0	37·8 ± 9·8	−3·5 ± 8·2	4

Transmural water transport

Water was absorbed from the incoming isosmotic solutions, and was secreted into the intestine when the incoming perfusion solutions were hyperosmotic. As a result of this the equilibrium osmolalities fell considerably in the hyperosmotic perfusion solutions. It was slightly lower than plasma osmolality in the isosmotic perfusion experiments both in normally hydrated and dehydrated birds (Table 3). The water absorption in isosmotic experiments with NaCl, KCl, and sucrose is reported in Table 6. The water absorption per sodium ion absorbed in isosmotic NaCl perfusion experiments is larger in the present experiments: 5·0 ± 0·4 μl./μequivalent than in the domestic fowl where 1·1 μl./μequivalent was found in the normally hydrated birds, 1·5 μl./μequivalent in the dehydrated birds (Bindslev & Skadhauge, 1971*b*). This is an important difference between these two species.

For comparison with other experiments the apparent $Na^+ + Cl^-$ concentration of the absorbate was calculated to 385 m-equiv/l. This value is

only slightly hyperosmotic to plasma in agreement with the slight dilution of the perfusion fluid in isosmotic perfusion experiments (Table 3).

The water transport into the lumen in the hyperosmotic experiments was used to calculate an apparent osmotic permeability coefficient with the osmotic difference from lumen to plasma calculated as the arithmetic mean of incoming and equilibrium fluid osmolalities. The result is reported in Table 7. The osmotic permeability coefficient seems to decrease with increasing osmotic difference. Such rectification has previously been found in the gall-bladder (Diamond, 1966).

TABLE 6. Solute-linked water absorption from isosmotic perfusion solutions (mean ± S.E.)

	μl./kg.hr	μl./μequiv $Na^+ + Cl^- + K^+$
NaCl	442 ± 31	2·7
KCl	337 ± 60	2·4
Sucrose	173 ± 75	2·3

TABLE 7. Osmotic permeability coefficients (mean ± S.E.)

μl./kg.hr.m-osmole	Mean Δ osmole
2·20 ± 0·29	306 ± 13
1·35 ± 0·19	404 ± 8
0·85 ± 0·19	446 ± 25

The values are lower than found in the domestic fowl where the osmotic permeability coefficient was 3·2 μl./kg.hr.m-osmole in normally hydrated birds, 3·6 μl./kg.hr.m-osmole in dehydrated birds (Bindslev & Skadhauge, 1971*a*).

DISCUSSION

In order to make the present experiments comparable with previous experiments in the domestic fowl (Bindslev & Skadhauge, 1971*a*, *b*; Skadhauge, 1967) identical perfusion fluids were used. In order to obtain more information from a limited number of experiments, osmotic permeability coefficients were also calculated from the hyperosmotic perfusion fluids with NaCl as the abundant solute instead of sucrose or raffinose. From the previous experiments (Bindslev & Skadhauge, 1971*a*, *b*) the solute-linked water flow was known to be negligible at very high osmolalities. This assumption would seem permissible also in the present experiments since a significant solute-linked water flow would give a deviation of the apparent osmotic permeability coefficient with higher osmolalities in the opposite direction of that observed.

The absorption of Na^+, K^+, and Cl^- followed the same pattern as in the

domestic fowl: higher intraluminal concentrations resulted, generally, in higher absorption rates. For sodium the results conformed well to saturation kinetics. A Na–K exchange as seen in the domestic fowl was not observed, and a high intraluminal K^+-concentration at unchanged Na^+-concentration, did not suppress the Na^+ absorption rate (compare sucrose and KCl perfusions, Table 5). This difference puts the Galah in a more favourable position for cloacal Na^+ resorption compared to the domestic fowl. It probably more than counterbalances the higher $C_{Na\frac{1}{2}}$. For chloride, saturation was not apparent in these experiments, but the variation in absorption rates at high concentrations was rather large.

The main difference from the domestic fowl is that more water follows ions in so-called solute-linked water flow. It is interesting to note that taken at face value the amount of water following the net $Na^+ + K^+ + Cl^-$ absorption seems to be the same (Table 6) regardless of the different flows of the three ions (Table 5) resulting from different luminal concentrations (Tables 2 and 3). The possibility of a solute-linked water flow following K^+ absorption is interesting and deserves further study, particularly since the cloacal epithelium according to the usual criteria would seem to fall in the category of 'tight' epithelia (Frömter & Diamond, 1972) with little solute-linked water flow. The physiological implication of the large solute-linked water flow in the Galah is that the cloacal transport parameters as determined in this study have such numerical values that the Galah can let the hyperosmotic urine formed in the dehydrated state into the cloaca without a further water loss. The dehydrated Galah forms ureteral urine at a rate of approximately 100 μl./kg.hr with a NaCl concentration of 50–100 mM, and K^+ concentration of 100–400 m-equiv/l. (Skadhauge, 1974*a*). In the coprodeum of Galahs caught in nature the contents had an osmolality around 700 m-osmole and ionic concentrations around 50 m-equiv/l. (Skadhauge, 1974*a*). This would seem to allow a resorption of approximately 70% of the NaCl coming to ureteral excretion and probably a slight resorption of water. This assumes an initial dilution and further orally resorption in the cloaca as calculated in detail by Skadhauge & Kristensen (1972). Although the dependence of solute-linked water flow upon the luminal osmolality is not known, an approximate estimate of the amount of sodium and water that needs to be absorbed in the cloaca if the cloacal sojourn of ureteral urine shall be without a net water loss can be made. Suppose a ureteral urine flow of 100 μl./hr of osmotic U/P ratio of 2·5 is diluted to plasma osmolality. This results in a flow into the intestine from plasma of 150 μl./kg.hr. A solute-linked water flow as large as accompanying the Na absorption in the sucrose experiments: 40 μequiv Na^+/kg.hr equivalent to 200 μl. H_2O/kg. hr would suffice to cover the initial dilution. It would thus seem possible for the Galah not to lose water

but perhaps save water in the cloaca at the expense of a reno-intestinal NaCl circulation. The reno-cloacal balance in the Galah thus seems to be as well adjusted as in the domestic fowl in spite of the higher renal concentrating ability. The high K^+ concentration in ureteral urine, and the demonstration in this study of K^+ absorption from luminal fluids of a high K^+ concentration further suggests studies directed at elucidation of the reflexion coefficient when K^+ is the abundant cation. Furthermore, the nitrogenous content of ureteral urine should be studied (Skadhauge, 1974*b*).

The few experiments do not permit evaluation of the possible effects of dehydration on the cloacal transport parameters.

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